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Cover Photograph: A *Bubulcus ibis* (Cattle Egret) seeking prey in a drifting floating meadow dominated by *Paspalum repens* (Water Paspalum) on the central Amazon River, west of Iranduba, Amazonas, Brazil, on 26 March 2015. Photograph © Floyd E. Hayes.

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Avian Use of Drifting Floating Meadows on the Central Amazon River of Brazil

Floyd E. Hayes^{1*}, Stephen Horvath², Erika R. Thalman¹, Dylan G. Turner¹, Zeko McKenzie³, and William K. Hayes³

Abstract - Floating rafts of aquatic macrophytes, referred to as floating meadows, are a conspicuous but seasonal component of Amazonian rivers. We searched for birds on 1,825 drifting floating meadows on the central Amazon River between Manacapuru and Manaus, Amazonas, Brazil. We observed 114 individuals of 12 species of birds, dominated by herons (Ardeidae) and vultures (Cathartidae). Bird abundance did not differ between floating meadows dominated by *Paspalum repens* (Water Paspalum) and *Pontederia crassipes* (Water Hyacinth); no birds were observed on those dominated by *Pistia stratiotes* (Water Lettuce). Birds were more abundant on larger floating meadows but were equally abundant on floating meadows within or beyond 100 m of shore. Floating snags within floating meadows provided convenient perches for foraging or resting birds. All bird species were carnivores or scavengers. Our results reveal that drifting floating meadows provide an important and previously underappreciated substrate for resting and feeding birds in Amazonia.

Introduction

Floating rafts of vegetation in lacustrine and riverine ecosystems vary greatly in their origin, structure, and size, and provide resources for animals opportunistically seeking shelter, food, rest, or reproduction (see review by Van Duzer 2004). Even small rafts of floating vegetation can provide a cornucopia of resources for many species of animals. For example, 48 species of vertebrates, including 43 species of birds, have been reported using small (<1 m²) floating nests of *Aechmophorus occidentalis* (Lawrence) (Western Grebe) and *Aechmophorus clarkii* (Lawrence) (Clark's Grebe) at Clear Lake, California, USA (Hayes et al. 2018, 2022).

Floating rafts of aquatic macrophytes, referred to as floating meadows, are a conspicuous but seasonal component of Amazonian whitewater lakes and rivers, but are much scarcer in blackwater lakes and rivers (Junk 1970). The floating meadows of Amazonia are colonized by a variety of invertebrates, fishes, amphibians, and reptiles (Araujo-Lima et al. 1986; Böning et al. 2017; Correa et al. 2008; de Matos et al. 2022; Dias et al. 2011; Ganança et al. 2021; Henderson and Crampton 1997; Henderson and Hamilton 1995; Hoogmoed 1993; Junk 1973; Petry et al. 2003; Ramalho et al. 2016, 2018; Schiesari et al. 2003; Upton et al. 2014). Although a variety of birds exploit the ephemeral resources available in floating meadows in Amazonia, only a few anecdotal accounts have been published (Cintra 2012, Cintra et al. 2007, d'Affonseca et al. 2012, Ferreira et al. 2021, Petermann 1997, Stotz et al. 1992). In this study we document the use of drifting floating meadows by birds along the central Amazon River of Brazil and compare the abundance of birds in meadows differing by dominant plant species, area, and distance from shore.

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Study Area and Methods

Study area

We surveyed birds on drifting floating meadows along a 99 km portion of the central Amazon River, classified as a whitewater river (Junk et al. 2011), between the confluence of the Manacapuru and Amazon Rivers in Manacapuru (03°18'S, 60°39'W) and the confluence of the Negro and Amazon Rivers in Manaus (03°08'S, 59°54'W), in Amazonas, Brazil. This section of the river is relatively wide (>5 km in some areas), with several large islands within the river and seasonally flooded wetlands and forests along the banks. The floating meadows are seasonal, developing rapidly as water levels rise and plateau (usually January–September), and gradually receding during the lowest water levels (usually October–December) (Junk 1970). The floating meadows are initially stationary, but as water levels rise, many are flushed from lakes and lagoons and drift downstream with the current (Junk 1970).

The floating meadows of this region are dominated by the grasses *Paspalum repens* P.J. Bergius (Water Paspalum) and *Echinochloa polystachya* (Kunth) (Aleman Grass), which comprise about 80–90% of the grasses (Junk 1970). Water Paspalum is dominant early during the flood pulse and Aleman Grass becomes equally common after heavy rains in May (Junk 1970). Floating meadows dominated by *Pontederia crassipes* Mart. (Water Hyacinth) and *Pistia stratiotes* Linnaeus (Water Lettuce) are also common (Junk 1970). Multiple species of plants occur in the larger floating meadows, but the smallest floating meadows are often formed of a single species. Floating snags (tree trunks and branches) of variable size are often associated with drifting floating meadows.

Survey methods

We surveyed birds from the deck of motorboats, about 1.5–4 m above the water, during 7 days on 27 March and 20 July 2014, 26 March 2015, 24 March 2016, and 1, 6, and 8 January 2017. Each survey was conducted during good light and clear weather. Binoculars were used to search for birds on floating meadows that were detached from shore and drifting downstream within 100 m of the boat. As we passed each meadow, we identified any species of bird present and counted the number of individuals of each species on each floating meadow. The amount of time surveying each meadow depended on its size but was not quantified, and each was surveyed only once. We also recorded the behavior of any birds observed foraging while associating with a floating meadow.

We classified each floating meadow as being dominated (>50% of area) primarily by either (1) Water Paspalum, (2) Water Hyacinth, or (3) Water Lettuce. The area of each floating meadow was estimated as either (1) <1 m², (2) 1–10 m², (3) 10–50 m², or (4) >50 m². The distance of each floating meadow from shore was estimated as either (1) <100 m or (2) >100 m. We lacked a global positioning system for precisely measuring distances from shore and were unable to accurately estimate distances in categories >100 m from shore. Although we attempted to survey most of the larger floating meadows, there were too many smaller floating meadows, many of which were <1 m², to survey all, therefore our data do not represent a random sample of different sized floating meadows differing in their distance from shore.

Statistical analyses

Because of the high frequency of zeros, we used the R package *pscl* v. 1.5.5 and *Stats_Zeroinfl* v 1.0.4 as extension modules in SPSS v. 28 to test alternative Poisson and negative binomial regression models (with default parameters) to assess whether meadow type, size, and distance from shore influenced bird numbers on the floating vegetation. We included

zero-inflated models, which incorporate two models to better control for structural zeroes (Artkins and Gallop 2007). We compared models using the Akaike information criterion (AIC) and calculated 95% confidence intervals (CIs) for incident rate ratios (IRRs; exponentiated β coefficients) using the formula $\text{Exp}(\beta \pm [1.96 * \text{SE}])$ (NCSS Statistical Software 2024). To better understand the difference between preliminary univariate analyses (not provided) and the regression outcomes, we conducted two additional chi-square goodness of fit tests (χ^2 statistic; Zar 2010). These included a 3×4 chi-square test for the association between meadow type and size and a 2×4 chi-square test for meadow distance and size. We computed Cramer’s V for these tests as a measure of effect size, with 0.1, 0.3, and 0.5 loosely interpreted as small, medium, and large effects, respectively (Cohen 1988).

Taxonomy

The taxonomy of plants and birds follows iNaturalist (www.inaturalist.org) and Remsen et al. (2023).

Results

We examined 1,825 floating meadows and observed 114 individuals of 12 species of birds (Table 1; Fig. 1). Vultures (Cathartidae) of three species were the most conspicuous birds, comprising 46.5% of all birds, including *Coragyps atratus* Bechstein (Black Vulture; 35.1%; Fig. 1C), *Cathartes burrovianus* Cassin (Lesser Yellow-headed Vulture; 10.5%), and *Cathartes aura* Linnaeus (Turkey Vulture; 0.9%) (Table 1). Herons (Ardeidae) of three species were also conspicuous, accounting for 43.0% of all birds, including *Bubulcus ibis*

Table 1. Mean (S.D.) and maximum number of bird individuals associating with three types of floating meadows on the central Amazon River, Amazonas, Brazil.

Species	Water Paspalum (n = 1108)	Water Hyacinth (n = 506)	Water Lettuce (n = 211)	Total bird individuals
	mean (SD) max	mean (SD) max	mean (SD) max	
Spotted Sandpiper	—	0.004 (0.09) 2	—	2
Wattled Jacana	0.004 (0.06) 1	0.002 (0.04) 1	—	5
Large-billed Tern	—	0.002 (0.04) 1	—	1
Cattle Egret	0.03 (0.24) 5	0.004 (0.09) 2	—	34
Great Egret	0.008 (0.10) 2	—	—	10
Snowy Egret	0.004 (0.06) 1	0.002 (0.04) 1	—	5
Green Ibis	0.001 (0.03) 1	—	—	1
Black Vulture	0.02 (0.39) 12	0.03 (0.47) 10	—	40
Turkey Vulture	—	0.002 (0.04) 1	—	1
Lesser Yellow-headed Vulture	0.01 (0.15) 3	—	—	12
Yellow-headed Cara-cara	0.002 (0.04) 1	—	—	2
Great Kiskadee	—	0.004 (0.09) 2	—	1
All bird individuals	0.08 (0.51) 12	0.05 (0.50) 10	—	114

Bonaparte (Cattle Egret; 29.8%; Fig. 1A), *Ardea alba* Linnaeus (Great Egret; 8.8%), and *Egretta thula* (Molina) (Snowy Egret; 4.4%; Fig. 1B) (Table 1). The remaining six species, all from different families, accounted for 10.5% of all birds, including *Jacana jacana* (Linnaeus) (Wattled Jacana; 4.4%), *Actitis macularius* (Linnaeus) (Spotted Sandpiper; 1.8%), *Milvago chimachima* Vieillot (Yellow-headed Caracara; 1.8%), *Phaetusa simplex* Wagler (Large-billed Tern; 0.9%), *Mesembrinibis cayennensis* J.L. Peters (Green Ibis; 0.9%), and *Pitangus sulphuratus* Swainson (Great Kiskadee; 0.9%; Fig. 1D) (Table 1). We did not observe any evidence that the noise of our motorboat or of other motorboats affected the results.

We observed eight species of birds in floating meadows dominated by Water Paspalum, eight species in those dominated by Water Hyacinth, and none in those dominated by Water Lettuce (Table 1). However, floating meadows dominated by Water Lettuce were always small, <10 m², in contrast with those of Water Paspalum and Water Hyacinth, which often exceeded 50 m² and sometimes exceeded 100 m².

A zero-inflated negative binomial (ZINB) regression model provided the best fit for the 1,814 cases having complete data with 45 iterations (log likelihood = -322.78, df = 9, $P < 0.001$). We used meadow size and distance from shore as predictors in the negative binomial (count) log model and meadow type for the zero-inflated logit model. For the count model, meadow size strongly predicted the number of birds present. Meadows 1–10 m²

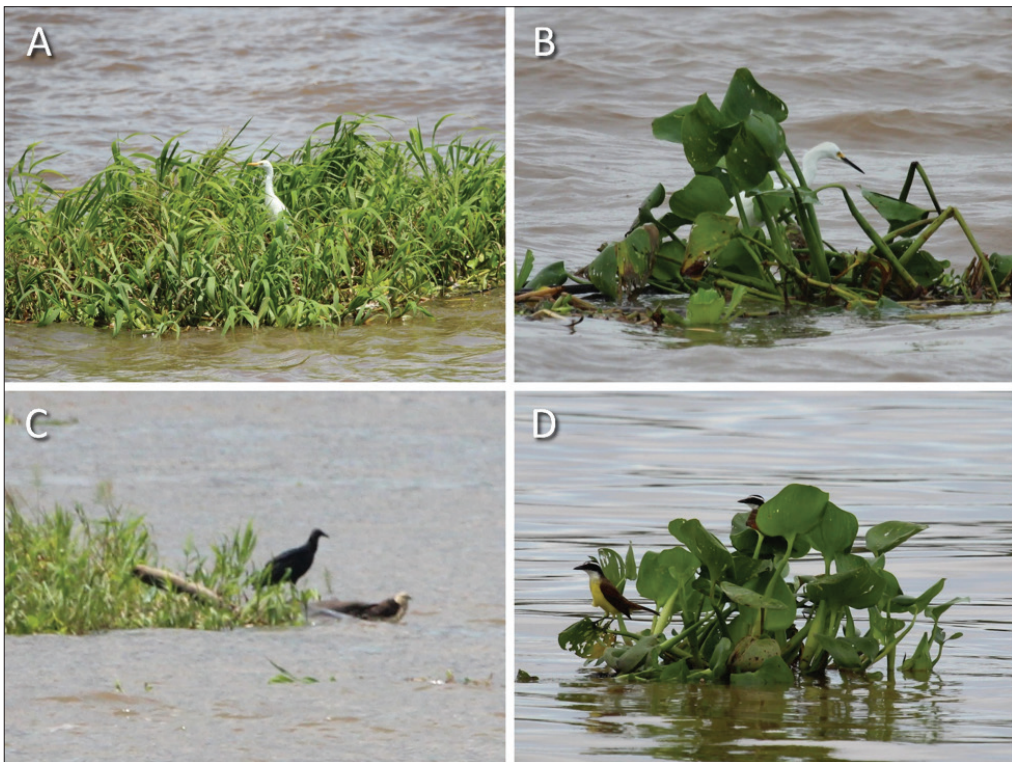


Figure 1. Examples of avian use of floating meadows drifting on the Amazon River of Brazil: (A) Cattle Egret in a floating meadow dominated by Water Paspalum; (B) Snowy Egret in a floating meadow dominated by Water Hyacinth; (C) Black Vulture and Yellow-headed Caracara on a snag in a floating meadow dominated by Water Paspalum; and (D) Great Kiskadees in a floating meadow dominated by Water Hyacinth. Photos by Floyd E. Hayes.

($z = 4.41$, $P < 0.001$, IRR = 9.96, 95% CI = 3.58–27.72), 10–50 m² ($z = 5.08$, $P < 0.001$, IRR = 23.50, 95% CI = 6.96–79.37), and > 50 m² ($z = 1.98$, $P = 0.048$, IRR = 11.83, 95% CI = 1.02–137.14) hosted roughly 10, 24, and 12 times more birds than meadows < 1 m²; meadows 10–50 m² hosted roughly twice as many birds as meadows 1–10 m² ($z = 2.123$, $P = 0.034$, IRR = 2.36, 95% CI = 1.07–5.20); and meadows > 50 m² had bird numbers similar to meadows 1–10 m² and 10–50 m² ($P > 0.56$; Fig. 2). Distance from shore approached significance ($z = -1.93$, $P = 0.053$), with the IRR of 0.50 (95% CI = 0.25–1.01), suggesting that roughly half as many birds were found on distant meadows compared to those closer to shore. Meadow type as the predictor in the zero-inflated model was non-significant ($P > 0.95$).

For univariate analyses, the three meadow types hosted different numbers of birds, but this resulted from confounding between meadow type and size ($\chi^2 = 711.11$, $df = 6$, $P < 0.001$, Cramer's $V = 0.44$), with water paspalum meadows more often classified as large and water hyacinth and water lettuce meadows more often classified as small. Meadow distance and size were also confounded, but to a lesser extent ($\chi^2 = 27.00$, $df = 3$, $P < 0.001$, Cramer's $V = 0.12$), with meadows close to shore more often comprising the smallest size class.

The smallest species of birds (Spotted Sandpiper, Wattled Jacana, and Great Kiskadee) that were most vulnerable to predators were not observed on floating meadows > 100 m

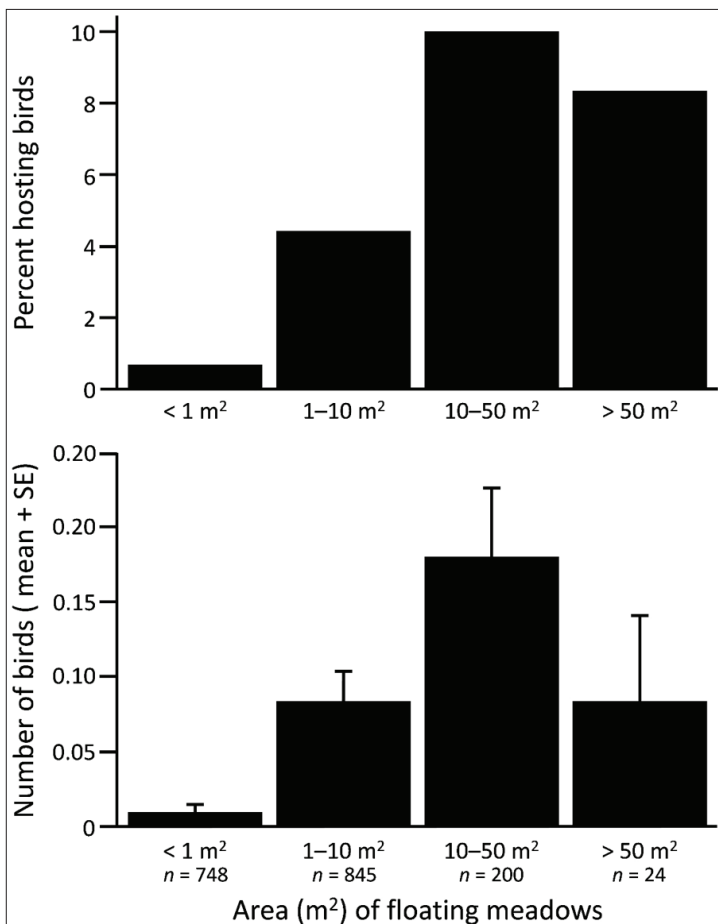


Figure 2. Proportion (%) of floating meadows of different sizes hosting birds and mean (+ S.E.) number of bird individuals on floating meadows of different sizes.

from shore. We often observed larger species of birds (mostly herons and vultures) on floating meadows near the middle of the river, > 1 km from shore.

Many birds appeared to be searching for food or resting. The Black Vulture, Lesser Yellow-headed Vulture, and Yellow-headed Caracara were observed scavenging on dead animals. Several birds were observed resting on floating snags within or at the edge of floating meadows, including the Spotted Sandpiper, Large-billed Tern, vultures, and Yellow-headed Caracara (Fig. 1C). We did not observe any evidence of birds nesting.

Discussion

Because ornithologists have focused primarily on studying the rich diversity of forest birds in Amazonian Brazil, the use of floating meadows by birds in the region is poorly documented, with only 23 species of birds previously reported. Stotz et al. (1992) reported huge flocks of two Nearctic landbird migrants, *Riparia riparia* (Linnaeus) (Bank Swallow) and *Hirundo rustica* Linnaeus (Barn Swallow), roosting in floating meadows within our study area at Marchantaria Island. Petermann (1997) studied the birds of Marchantaria Island and found the fewest number of bird species on sandbanks, followed by floating meadows, sandbar scrub, forest, and lakeside scrub. Unfortunately Petermann (1997) did not provide a list of all species observed in floating meadows, but he mentioned 14 species, including *Porphyrio martinica* (Linnaeus) (Purple Gallinule), *Porphyrio flavirostris* (Gmelin) (Azure Gallinule), *Laterallus exilis* (Temminck) (Gray-breasted Crake), *Jacana jacana* (Linnaeus) (Wattled Jacana), *Ixobrychus exilis* (Gmelin) (Least Bittern), *Ardea cocoi* Linnaeus (Cocoi Heron), Great Egret, Snowy Egret, *Megaceryle torquata* (Linnaeus) (Ringed Kingfisher), *Certhiaxis cinnamomeus* (Gmelin) (Yellow-chinned Spinetail), *Donacobius atricapilla* Swainson (Black-capped Donacobius), *Chrysomus icterocephalus* (Linnaeus) (Yellow-hooded Blackbird), *Sporophila castaneiventris* Cabanis (Chestnut-bellied Seed-eater), and *Sicalis columbiana* Cabanis (Orange-fronted Yellow-Finch). Petermann (1997) also reported Large-billed Tern and *Chordeiles nacunda* Vieillot (Nacunda Nighthawk) hawking for insects above floating meadows, but not within floating meadows.

Cintra et al. (2007) and Cintra (2012) listed six species of birds using floating meadows in blackwater lakes west of our study area, including four additional species: *Aramides cajaneus* (Müller) (Gray-cowled Wood-Rail), *Heliornis fulica* (Boddaert) (Sungrebe), *Tigrisoma lineatum* (Boddaert) (Rufescent Tiger-Heron), and *Butorides striata* (Linnaeus) (Striated Heron). d’Affonseca et al. (2012) reported four of the above mentioned species using floating meadows in the vicinity of Manaus. Ferreira et al. (2021) quantified the use of “aquatic macrophytes,” including floating meadows, by eight species of herons in lakes east of our study area, with three additional species: *Nycticorax nycticorax* (Linnaeus) (Black-crowned Night-Heron), Cattle Egret, and *Egretta caerulea* (Linnaeus) (Little Blue Heron).

The previous studies did not state whether the birds were observed on stationary or drifting floating meadows, but because Cintra et al. (2007), Cintra (2012), and Ferreira et al. (2021) studied birds on lakes and Petermann (1997) studied birds on a riverine island, all previous reports were likely based on observations at stationary floating meadows. Our study provides the first report of birds on drifting floating meadows. We observed four of the previously reported species of birds (Wattled Jacana, Cattle Egret, Great Egret, and Snowy Egret) using floating meadows. Eight of our bird species had not been previously reported using floating meadows in Amazonian Brazil (Spotted Sandpiper, Large-billed Tern, Green Ibis, Black Vulture, Turkey Vulture, Lesser Yellow-headed Vulture, Yellow-headed Caracara, and Great Kiskadee), increasing the total number of species to 31. Undoubtedly further research will increase the number of bird species using floating meadows in Amazonia.

Because floating meadows are available for only a portion of the year and the herbaceous plants provide a flimsy platform for nesting birds, Petermann (1997) regarded the “relative habitat preference” of birds for floating meadows as “low.” Petermann (1997) stated that the Wattled Jacana was the most common bird and that it often nested in floating meadows (presumably stationary) at Marchantaria Island. We did not observe any evidence of birds nesting in floating meadows. Given the hazards of strong winds, large waves, and increased vulnerability to predators in floating meadows that drift downstream, it is doubtful that birds ever nest in them.

Our data reveal that birds are much more common on floating meadows dominated by Water Paspalum and Water Hyacinth than on Water Lettuce. Water Paspalum and Water Hyacinth form larger floating meadows than Water Lettuce, due to their longer, sturdier, and more sprawling stems and roots, which connect the plants together and provide more perches and stronger support for birds than the smaller stems and roots of Water Lettuce. Furthermore, more prey are available in meadows dominated by Water Paspalum and Water Hyacinth than in meadows dominated by Water Lettuce, which has been demonstrated for fishes (Petty et al. 2016) and frogs (Ganança et al. 2021).

The greater abundance of birds on larger floating meadows is unsurprising given that species richness and habitat area are positively correlated for many taxa in a variety of habitat islands (Connor and McCoy 1979). Pires et al. (2023) experimentally demonstrated that more species of fishes are attracted to larger floating meadows in our study area.

The equal abundance of birds in floating meadows within or beyond 100 m of shore indicates that many birds, at least the more common larger species less vulnerable to predation, readily disperse > 100 m of open water, and some more than > 1 km, to forage on floating meadows despite an abundance of resources along the shore. However, all of the floating islands in our study were drifting. Stationary floating meadows along the shore are likely used more frequently by birds, especially by smaller species that forage, shelter, and nest in taller terrestrial vegetation along the shore (Petermann 1997).

Several of the birds we observed were perched on snags in floating meadows. Floating snags of various sizes are ubiquitous along the Amazon River and often occur within or at the edges of floating meadows, providing an important resource as convenient perches for foraging or resting birds. However, floating snags not associated with floating meadows were preferred by *Rynchops niger* Linnaeus (Black Skimmer), *Sternula supercilialis* (Vieillot) (Yellow-billed Tern), Large-billed Tern, and *Phalacrocorax brasilianus* (Gmelin) (Neotropic Cormorant) (personal observations).

Floating meadows attract a variety of invertebrates and small vertebrates, providing ephemeral resources for carnivorous or scavenging birds. Seven of the 12 species of birds in our study presumably forage for invertebrates or small vertebrates in floating meadows, including Spotted Sandpiper, Wattled Jacana, Cattle Egret, Great Egret, Snowy Egret, Green Ibis, and Great Kiskadee. Ferreira et al. (2021) demonstrated that floating meadows were the most important habitat for five species of herons, providing convenient access to aquatic prey. We observed three species, Black Vulture, Lesser Yellow-headed Vulture, and Yellow-headed Caracara, scavenging on dead animals in floating meadows. The Turkey Vulture also scavenges on dead animals. The Large-billed Tern feeds on fish in open water rather than in floating meadows, but also feeds on insects above floating meadows (Petermann 1997); the one we observed was resting on a snag within a floating meadow. Although we did not observe any granivorous species of birds, two species (Chestnut-bellied Seedeater and Orange-fronted Yellow-Finch) plus an omnivore (Yellow-hooded Blackbird) were reported by Petermann (1997).

Because the macrophytic plants of floating meadows modify the physical environment by providing physical structures that limit photosynthesis, limit the oxygenation of water, and provide shelter, food, and rest for other organisms, including birds, they can be regarded as autogenic ecosystem engineers (Jones et al. 1994, Emery-Butcher et al. 2020). Our results reveal that drifting floating meadows dominated by Water Paspalum and Water Hyacinth (but not Water Lettuce) provide an important and previously underappreciated substrate for resting and feeding birds in Amazonia. Further studies are needed to better understand the diversity and ecology of birds exploiting the resources of floating meadows, not just in Amazonia but also in other parts of the world.

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